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Familial Association, Nymphal Development and Population Density in the Australian Giant Burrowing Cockroach, *Macropanesthia rhinoceros* (Blattaria: Blaberidae)

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ABSTRACT—The Australian giant burrowing cockroach *Macropanesthia rhinoceros* was studied with respect to population density, familial association and nymphal development. These, and other field observations, were made in the eucalypt open woodlands of northeastern Queensland at intervals from October 1987 to October 1989. Three hundred one nest burrows were excavated in 16 plots (each 8 m × 4 m), and 329 adults and lone nymphs (old and middle age) were examined. Thirty-two families, which consisted of a group of young nymphs together with either an adult pair or an adult female were found in and around the plots from Nov. 1987 to Mar. 1988. The cockroaches form family groups in the early spring and close adult female-offspring relationships persist for about half a year. The nymphs reach the sixth or seventh instar by the autumn. Then they disperse from their natal burrows to make their own.

INTRODUCTION

The cockroaches (Blattaria) are of special interest among the presocial insects because they are closely related to the Isoptera (termites), all of whose members are eusocial [1]. The ovoviviparous Blaberidae are frequently subsocial. Roth and Willis [2] described the familial associations of 15 species of cockroaches, mostly ovoviviparous, that probably brood their young. Schal *et al.* [3] discussed the reproductive tactics of cockroach females and males. Brood care is generally seen in aggregations of newly-hatched offspring around their mother, the mother to some extent facilitating the nymphal aggregation by remaining immobile for varying periods of time [4]. In addition, some species dwelling inside wood, and feeding on it, have a monogamous family life. The link between adults and nymphs in the wood-feeding cockroaches *Cryptocercus* (Cryptocercidae) and *Salganea* (Blaberidae, Panesthiinae) is long lasting, and can last the whole nymphal life [5–8]. The appearance of a monogamous family structure in wood-feeding cockroaches and termites is a true convergence [9, 10].

The giant burrowing cockroach *Macropanesthia rhinoceros* is an ovoviviparous blaberid that displays brood care and is the largest and bulkiest blattarid in Australia [11]. The body length of the largest adult male reaches about 8 cm and the live weight reaches 30 g. However, little information has been available to date on the ecology in the field. Only Day [12] notes as follows: "Little is known of the life history of *Macropanesthia,* but some details have been supplied by Mr. W. A. Henson. The roaches are infrequently observed during the dry season from March to October. They burrow quite deeply, about two feet below the surface of sandy soil in stands of cypress pine (*Callitris* sp.). They make a nest of dead leaves, grass roots, etc., frequently among the pine roots. The young nymphs rarely appear above ground, but following rain the adults burrow to the surface, especially at night".

The present paper deals with familial associations, development of nymphs, population density and other field observations of the giant burrowing cockroach, *M. rhinoceros* in the eucalypt open woodlands of northeastern Queensland. Studies of the distribution pattern of nests and the material cycles (carbon and nitrogen) in ecosystem medi-

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ated by the cockroach will be published elsewhere.

MATERIALS AND METHODS

The giant burrowing cockroach belongs to the Panesthiinae most species of which are found primarily in the Indo-Malayan and Australian regions [11]. In the Australian continent, the subfamily is largely restricted to the eastern part including species which live in and feed on dead wood in rain forests (e.g. *Panesthia* and *Ancaudellia*) and species which inhabit underground burrows in open woodlands or grasslands. (e.g. *Macropanesthia* and *Geoscapheus*). Almost all of these taxa are found in Queensland but are comparatively poorly represented in other states. *M. rhinoceros* occurs in rather dry areas around the tropical rain forests of northeastern Queensland from Cooktown to Rockhampton along the Great Dividing Range [11].

The study sites are located in the open eucalypt woodlands near Smith Creek about 12 km southwest of a town, Mount Garnet (17.41S, 145.07E, altitude 680 m), and near Uramo, about 10 km east of the town in northeastern Queensland. The forest and soil types of Smith Creek and Uramo are not different. The soil is sandy and not developed, the thickness of the whole (A) layer being about 10 cm of which litter (Ao) layer is under 1 cm. The dry season is from May to November and wet season is from December to April and these directly influence the water con-

TABLE 1. Number of nest burrows, cockroaches and social units per plot of 32 m^2 (8 m×4 m) in 16 plots

Plot No.	Place of survey	Date	Season (temp.)[1]	No. of nests	No. of cockroaches[2]		Social unit	
					Male	Female	Pair[3]	Family[4]
1	Smith	23–28 Oct. '87	Spring	28	15	15	1	1
2	Uramo	32– 2 Nov.	(29°C)	18	7	12	0	5
3	Uramo	13–15 Dec. '87	Summer	20	7	14	1	4
4	Smith	16–18 Dec.	(31°C)	29	12	20	3	1
5	Smith	12–13 Mar. '88	Autumn	14	8	6	0	0
6	Smith	14 Mar.	(26°C)	11	4	8	1	0
7	Uramo	15–16 Mar.		18	13	10	3	3
8	Uramo	17 Mar.		26	14	17	5	2
9	Smith	15–17 Jul. '89	Winter	13	6	9	2	0
10	Uramo	17–19 Jul.	(21°C)	21	11	13	3	0
11	Uramo	20 Jul.		9	4	5	0	0
12	Smith	21–22 Jul.		16	7	10	1	0
13	Uramo	20– 2 Oct. '89	Spring	21	11	11	1	0
14	Smith	3– 4 Oct.	(26°C)	17	5	14	2	0
15	Uramo	5– 7 Oct.		30	17	14	1	0
16	Smith	8 Oct.		10	5	5	0	0
Total (in average)				301 (18.8)	146 (9.1)	183 (11.4)	24 (1.5)	16 (1.0)

[1] Mean temperature in the bottom of nest burrows. The temperature observed in all nests during the same season did not vary more than the 1°C precision allowed by the thermometer. Thus no standard deviation could be calculated.

[2] These figures include the number of adults, sub-adults and large nymphs, not include young numphs under sixth instar.

[3] Adult pairs (male and female)

[4] Families consiting of a group of young mymphs together with an adult pair, and families with an adult female and young numphs.

tent of the soil. The sandy soil is compacted in the dry season and is soft but not sticky in the wet season. The largest tree measured was about 30 cm in diameter and ca. 25 m high. Grasses are common on the woodland floor and used for pasture in rainy season. Litter accumulation was 263 g/m^2 near Smith Creek (n=11, leaf litter=124 ±76 g, small branch litter=139±82 g) and was 126 g/m^2 near Uramo (n=11, leaf litter=68±32 g, small branch litter=58±52 g).

The field studies and collections were made on five occasions from October 1987 to October 1989 (Table 1). Sixteen plots (each 8 m×4 m) and some areas around the plots were investigated. The surface of the sandy soil in plots was removed to a depth of about 10 cm using a scoop, and then, the entrance holes of burrows were mapped. A trench about 50 cm wide and 50 cm deep was then dug carefully along the nest burrow using shovel for the heavy work, and a trowel for the finer work. The burrows descend about 40 cm deep in a broad curve and have a small chamber at the bottom where the adults live and rear their nymphs. We opened 301 nest burrows in and around the plots and examined the cockroaches, food storages, feces, predators and sometimes guests in the burrows. These items were dried for about 5 days before being weighed. Some samples of insects and eggs were kept in 80% alcohol. Eggs in ovaries and brood pouches were studied by dissection of females in July and October 1989.

Nest temperature was measured by inserting a mercury thermometer into the terminal portion of nest prior to excavating it. The thermometer was calibrated in 1°C intervals, and all observations were made during the day.

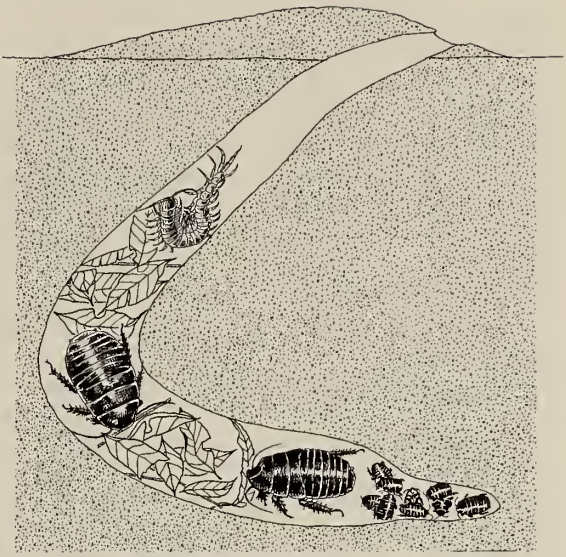

Fig. 1. Schematic diagram of a nest burrow of the Australian giant cockroach *Macropanesthia rhinoceros* with an adult pair, young nymphs and a predator (centiped) in spring. Leaf litters are transported by adults from ground surface at night. The tough adult external skeleton may protect against centipede attack. (drawn by Y. Ohira)

RESULTS

Nest burrows

Figure 1 shows a schematic presentation of a nest burrow with an adult pair, nymphs and a predator (centipede) in spring. The size of the nest burrow is about 1 m long and 40 cm deep, and it descends at about a 20° angle. The semi-circular cross-section of the burrow is 4–15 cm in diameter and has a plastered wall. The entrance is concealed in raised loose dirt in the dry season. Two examples of the distribution of nest burrows in the plots No. 4 and No. 8 are shown in Figure 2. Most nest burrows are more or less curved. In a few cases (e.g., Nest No. 30 in Plot No. 4), the burrow was in the form of a spiral. I did not observe the case in which two burrows are connected. The distribution pattern of nest burrows is almost uniform. About 10% to 50% of burrows in a quadrat appeared to be abandoned. In those burrows, fungi were usually found growing on the remaining feces and food. The cockroaches prefer litter on the ground as food, which contains dead leaves, woods and grasses. A cockroach grasps the food in its mandibles and transports it walking astride of it. Foraging activity apparently takes place mostly at night in the rainy season. We believe the cockroaches play an important role in litter turnover (unpublished).

Population density

Table 1 shows the abundance of nest burrows, the number of individuals per plot and the sociality

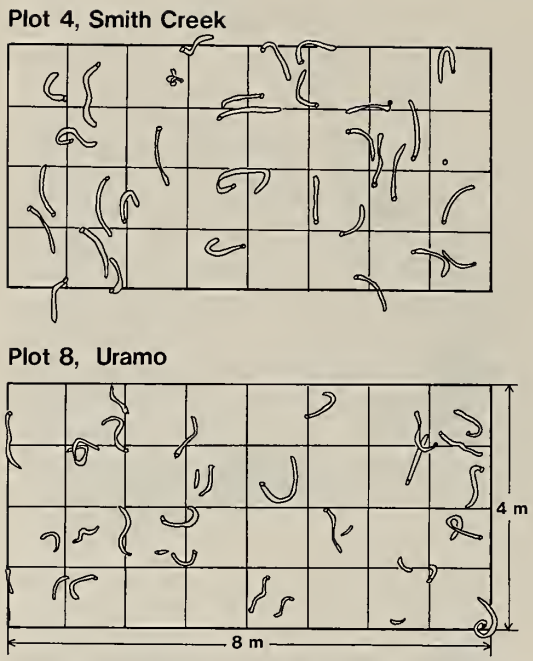

Fig. 2. Two examples of the distribution of nest burrows in the plots No. 4 and No. 8. Most net burrows are more or less curved. The distribution pattern of nest burrows is almost uniform. Connection between two nest burrows is rare. Several (approx. 10%) of burrows in a plot appeared to be abandoned.

of groups. In the plot (No. 4) in which nest burrows were most abundant, there were 29 burrows and 32 large cockroaches. No cases were seen in which three or more adults occured together in a burrow. In each plot, a mean of there was 19 burrows, and 1.5 pairs, 1.01 families were observed, 9.1 males and 11.4 females live in burrows.

Table 2 summaries the composition of the groups found in the same burrows and shows the total number of individuals including young nymphs which were found with adult pair or adult females. One hundred forty seven adults, 179 non-adults (sub-adults and old nymphs) and 321 young nymphs were collected from 16 plots. The sex ratios of adults and non-adults were slightly lower than 0.5 (males: females=1:1). The sex ratio of young nymphs was not measured.

Familial composition

Thirty two families consisting of a group of young nymphs together with an adult pair or an adult female were observed in and around the plots from Nov. 1987 to Mar. 1988 (Table 3). Nymphs are housed in the deepest portions of the burrows (Fig. 1). Table 4 summarizes number of eggs in ovaries or the brood sac, and the brood sized of families. In late October on 1987 (late spring), eleven families were observed with an

Table 2. Composition of the groups collected in 16 plots and number of cockroaches per two or four plots

Category	Plots No. 1, 2 23–2 Nov. 1987	Plots No. 3, 4 12–18 Dec. 1987	Plots No. 5–8 12–17 Mar. 1988	Plots No. 9–12 15–22 Jul. 1989	Plots No. 13–16 30–8 Oct. 1989	Total
Single (adult ♂)	0	2	1	9	14	26
Single (non-adult ♂)	19	12	28	13	20	92
Single (adlult ♀)	1	2	11	21	20	55
Single (non-adult ♀)	19	23	15	10	20	87
Pair (1♂+1♀)	1	4	9	6	4	24
Family (♀+nymphs)	4	5	5	0	0	14
Family (♂♀+nymphs)	2	0	0	0	0	2
No. of young nymphs*	157	89	75	0	0	321
Total no. of indv.**	206	141	153	65	82	647
Sex ratio (♂/♀+♂)	0.45	0.35	0.49	0.46	0.44	

* Total number of nymphs consisting of a group with an adult pair or an adult female
** adults and non-adults not including young nymphs

Table 3. Family compositions (Adult and young nymphs) of 32 colonies of *M. rhinoceros* in and around the plots

Date of survey	Presence of adult(s)	Number of nymphs	
		(instar)	(number)
23 Oct. '87	♀	1st instar	29
	♀	1st instar	13
30 Oct.	♀, ♂	1st instar	16
	♀	1st instar	17
31 Oct.	♀, ♂	1st instar	32
	♀	1st instar	32
	♀	1st instar	28
	♀	1st instar	20
2 Nov.	♀	1st instar	29
4 Nov.	♀, ♂	1st instar	24
	♀, ♂	1st instar	22
13 Dec. '87	♀	2, 3rd instars	20
	♀	2, 3rd instars	15
	♀	3, 4th instars	13
15 Dec.	♀	2, 3rd instars	22
	♀	3rd instar	21
17 Dec.	♀	2, 3rd instars	11
19 Dec.	♀	3rd instar	24
	♀	3rd instar	17
	♀	3, 4th instars	19
	♀	3, 4th instars	18
	♀	3, 4th instars	7
15 Mar. '88	♀	5, 6th instars	19
	♀	5, 6th instars	17
	♀	5, 6th instars	12
17 Mar.	♀	5, 6th instars	11
	♀	6th instar	17
18 Mar.	♀	5, 6th instars	18
	♀	5, 6th instars	16
	♀	5, 6th instars	13
	♀	5, 6th instars	10
	♀	6th instar	15

average brood size of 22.8. Interestingly, in only four of thirty two cases were adult males *M. rhinoceros* found in familial associations with nymphs and females. These nests were excavated in the spring of 1987. In all other cases (n=28), only adult females were found in familial associations with nymphs. In middle December of 1987 (summer), nymphs had reached third or fourth instar and brood size decreased to a mean of cockroaches 17.0. No adult males were observed in family groups in the summer. In middle March on 1988 (autumn and rainy season), nymphs had reached the fifth or sixth instar and the mean brood size was 14.8. In late July of 1989 (winter), no families with young nymphs were observed.

M. rhinoceros is a ovoviviparous cockroach and new nymphs emerge from the brood sac of female in spring. All eggs in the ovaries or sacs of each adult female were removed and weighed as a group in July 1989. The number of eggs in ovaries is 23.8 on average as shown in Table 4. The body length of pre-emergent nymph in brood sac is about 1 cm. The newly-emerged cockroaches might appeared first in middle October (late spring).

Growth of nymphs

The new nymphs eat leaf litter stored in nest burrow by the adults. All data on the size of young nymphs living in nest burrows with adults in late October 1987, mid December 1987 and mid March 1988 are presented in Figure 3. Nymphs seem to grow synchronously, and disperse from their nest burrow in the sixth instar, after which they live a solitary existence until they become adults. The body length of adults is about 7–8 cm. The size distribution of pronotum widths of old nymphs and adults living in a solitary life or forming a pair are

Table 4. Number of eggs in ovaries or brood sac, and brood size of *Macropanesthia rhinoceros*

Date of survey	Season	No. of female with offsprings	Age of offsprings	Brood size	
				Mean±S.D.	Range
23 Oct.–4 Nov. '87	Spring	11	1st instar	23.8±6.7	13–32
13–19 Dec. '87	Summer	11	3–4th instar	17.0±5.1	7–24
12–18 Mar. '88	Autumn	10	5–6th instar	14.8±3.1	10–19
15–22 Jul. '89	Winter	16	Eggs in ovary	23.8±5.3	13–33
20 Sep.–8 Oct. '89	Spring	17	Eggs in brood sac	22.8±4.6	14–29

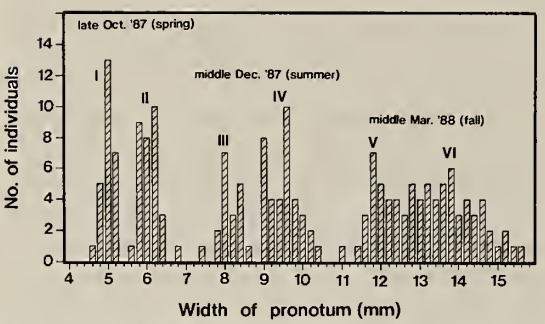

FIG. 3. The size distribution of pronotum widths of young nymphs living in nest burrows with adults on late Oct. '87, middle Dec. '87 and middle Mar. '88. Nymphs seems to grow synchronously. Instars are denoted by Roman numerals.

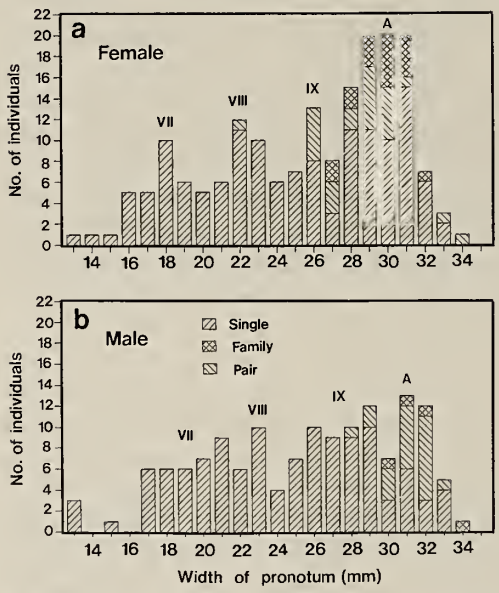

FIG. 4a, b. The size distribution of pronotum widths of old nymphs and adults living solitarily, in pairs, and in familial associations. A few large nymphs and some adults form pairs, and some adults have young numphs in their nest burrows. Data from nest burrows not censused in plots at Smith Creek and Uramo is included in these figures. A little old-nymphs and some adults make pair life, and some adults have young nymphs in their nest burrows. Instars are denoted by Roman numerals.

shown in Figure 4a, b.

I estimated how many instars the cockroaches have in nymphal stage on the basis of the size distribution of pronotum widths in Figure 3 and 4a, b. Sexual dimorphism of *M. rhinoceros* is not apparent until the fifth or sixth instar. After this point the differences in pronatal shape become clear. A total 597 of predispersal nymphs and 141 free-living nymphs from 16 plots and adjacents areas were investigated. Nine peaks can be recognized from Figures 3 and 4. The cockroach probably has nine instars in the nymphal stage. Nymphs live a solitary life from the seventh to ninth instar, or in a few cases from the sixth instar stage. Some adults form pairs which have young nymphs in the nest burrows as shown Figure 4a, b.

DISCUSSION

Gautier *et al.* [10] discussed the relationship between ecology and social behavior in cockroaches, and stated the importance of research for correlations between habitat parameters and social characteristics. Cockroaches may use any one or a combination of the following proximate and evolutionary defensive tactics: concealment, evasive behaviors, protective or aposemantic colouration, chemical defence, disturbance sound production, and fighting [3]. Species of *Pycnoscelus, Arenivaga, Epilampra, Geoscapheus, Blaberus, Hyporhicnoda, Eublaberus,* and *Brysotria* cited in Schal *et al.* [3] burrow into the substratum during the inactive period, or in response to disturbance. I consider that *Macropanesthia* use apparently the burrowing behavior for defensive and protective tactics against natural enemy and severe climate.

Why are the adults of *M. rhinoceros* so large, and why do they have a long-lasting family life? To answer these questions from ecological point of view, natural enemies comprise the most important among many habitat parameters. Field observations indicated that the main natural enemies are centipedes and large spiders. Both animals were observed frequently in the field, and I observed a large centipede (*Ethomostigmus* sp., body length is about 18 cm) feeding on a solitaly nymph in a nest burrow. Centipedes can not eat adult cockroaches, because the tough adult external skeleton protects cockroaches against centipede attack. This observation was confirmed in a preliminary manner with a laboratory experiment. Large spiders (Theraphosidae, body length is about 4.5 cm) were found several times in nest

burrows where no cockroach was found. It is possible that nymphs were eaten by the spiders. It is unlikely that the spiders prey on adult *M. rhinoceros,* because these insects are larger and more heavily armored than the spiders. During early nymphal stages, when natural enemies invade a nest burrow, adult cockroaches defend themselves and their offspring. Adults may be able to block a nest burrow against the enemy by using its robust body (Fig. 1). I have seen many large ditches about 20 cm deep on the surface of ground in the field; possibly resulting wild pigs or marsupials (bandicoots?) which were foraging for the cockroaches in shallow burrow, but detail are unknown.

Obviously the shape of *M. rhinoceros* has adapted for life in dry sandy areas. The cockroach has a smooth, flattened body, finger-like spines on front legs (reminiscent of those of a mole), a shovel-shaped pronotum, and completely lacks wings. These aspects of body shape may represent adaptations for digging in sandy soil. Day [12] studied on internal anatomy and histology of this cockroach in comparison with a relatively small one, *Blattella germanica* (weight, approximately 0.06 g) and concluded that gravity, diffusion, and the area available for secretion and absorption are not factors limiting the size of *M. rhinoceros,* and that the specializations observed in *M. rhinoceros* are related to its burrowing habits and food.

Some males of *Macropanesthia* were observed to live with a female and first instar nymphs in early spring (Fig. 4a). This is similar to the monogamous family life observed in xylophagous species such as *Cryptocercus punctulatus, Salganea taiwanensis* and *S. esakii* [6–8]. But the familial association of *M. rhinoceros* does not continue for long, in that all males leave the families when nymphs have reached to the second instar. It is possible that the males search for other females for mating.

The growth of nymphs is synchronously as shown in Figure 3. This could be due to the fairly prolonged dry period in this locality, which limits the timing of reproduction. And the steady environmental condition in deep burrow is also important. I observed that the temperature of burrow is warmer than ambient temperature in the early morning on mid July in 1989 (in mid-winter, 21°C:7°C), and that of the burrow is cooler than the ambient temperature in the afternoon on mid December in 1987 (in mid-summer, 31°C:44°C). It can be said that the deep burrows buffer the roaches from severe temperature change. Therefore, the nymphs can grow synchronously. However the factors triggering the dispersal of middle-aged nymphs from their mother's nest remain unclear.

Roth [11, 13–15] divided the Panesthiinae into five tribes: Panesthiini, Ancaudeliini, Salganeini, Caepariini and Geoscapheini. The first four tribes all live in and feed on dead wood. All species in the Geoscapheini, which includes *Macropanesthia,* live in burrows and feed on litter from the ground surface. On the basis of the differences in reproductive behavior observed by Rugg and Rose [16] and in morphology and habits as noted by Roth [11, 15], Rugg and Rose [17] believe that the Geoscapheini represent a sister-group to the other tribes and should be ranked as a subfamily. I consider the Geoscapheini, which is composed of four genera (*Macropanesthia, Parapanesthia, Geoscapheus* and *Neogeoscapheus*), derived from the ancestor of a xylophagous cockroach similar to the rain forest Panesthiini, which became secondarily adapted for savannah life. The familial bond of Geoscapheini with adult and offspring in the ground were strengthend at the same time, when savannah life was adopted.

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